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REVIEW

TUNING IN TO FISH SWIMMING WAVES: BODY FORM, SWIMMING MODE AND MUSCLE FUNCTION

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Summary

Most fish species swim with lateral body undulations running from head to tail. These waves run more slowly than the waves of muscle activation causing them, reflecting the effect of the interaction between the fish's body and the reactive forces from the water. The coupling between both waves depends on the lateral body shape and on the mechanical properties of the tail. During steady swimming, the length of each myotomal muscle fibre varies cyclically. The phase relationship between the strain (muscle length change) cycle and the active period (when force is generated) determines the work output of the muscle. The muscle power is converted to thrust either

directly by the bending body or almost exclusively by the tail, depending upon the body shape of the species and the swimming kinematics. We have compared the kinematics and muscle activity patterns from seven species of fish with different body forms and swimming modes and propose a model which yields a consistent pattern, with at least three extremes. Subtle tuning of the phase relationship between muscle strain and activation cycles can lead to major changes in the way muscles function in different swimming modes.

Key words: fish, myotomal muscle, swimming.

Introduction

To swim at a steady speed a fish must produce power, primarily to overcome drag. This power is generated by the myotomal muscle on either side of the body. A wave of muscle activation/contraction (detected as an electromyogram, EMG) passes alternately down each side of the body from head to tail. A wave of curvature also travels down the body, as a result of the combined effects of muscle activity, the arrangement and physical properties of the myosepta and skeletal elements, and the interaction between the fish's body and the reactive forces from the water in which it moves (for a review, see Videler, 1993). The role of the passive myoseptal and skeletal elements is important, but beyond the scope of this review. Because of the interaction between the body and the water, the coupling between muscle activity and body curvature depends upon the characteristic shape of each fish species. The power generated by muscle contraction is converted to thrust, either along the length of the fish, or at the tail, depending upon the swimming mode. The relationship between the waves of muscle activity and body curvature also depends upon the swimming mode adopted by the fish. Muscle fibres lengthen and shorten rhythmically during steady swimming. The timing of muscle activity relative to the phase of the strain cycle determines the force, work and power output of the muscle. Just how body

shape, kinematics and muscle timing come together to generate thrust is still in debate (Altringham *et al.* 1993; Rome *et al.* 1993; Wardle and Videler, 1994; Johnson *et al.* 1994), and no unifying theory has been proposed to explain either the different patterns of EMG and strain observed or the different patterns of muscle function. We have compared seven species of fish with very different body forms and swimming modes. Our analysis shows that the apparently conflicting results of recent work can be reconciled in one consistent pattern.

Background

Electromyography, in conjunction with a kinematic analysis of body shape changes, has been used for many years to address the problem of how fish use their muscle to swim (e.g. Blight, 1976; Grillner and Kashin, 1976; Johnston *et al.* 1977; Bone *et al.* 1978; van Leeuwen *et al.* 1990; Wardle and Videler, 1993). More recently, using isolated muscle fibres, the information derived from this sort of analysis has been used to simulate, *in vitro*, the *in vivo* operating conditions, yielding previously unobtainable information (Altringham *et al.* 1993; Rome *et al.* 1993; Johnson *et al.* 1994). What have these studies told us to date? They tell us that muscle activity

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alternates from one side of the fish to the other (e.g. Blight, 1976), that the slow (red) muscle is used to power slow sustainable swimming and that, as swimming speed increases, there is a progressive recruitment of the fast (white) muscle (e.g. Johnston *et al.* 1977; Bone *et al.* 1978). The power requirements of swimming increase roughly with the cube of the swimming speed (Webb, 1978), and force increases with the square of swimming speed. The cross section of muscle used to swim is proportional to the force needed (Wardle, 1985). Not surprisingly, the bulk of the myotomal muscle is made up of fast fibres, which generate higher power at higher tailbeat frequencies than slow muscle fibres (Altringham and Johnston, 1990a).

Differences exist in details of the timing between the waves of EMG activity and body curvature in the different fish that have been examined. Although these differences have been known for some time, their significance is only now beginning to be fully appreciated and debated (Altringham *et al.* 1993; Rome *et al.* 1993; Wardle and Videler, 1994; Johnson *et al.* 1994). A combined kinematic and dynamic analysis of steady swimming in eel and saithe by Hess (1983), Videler and Hess (1984) and Hess and Videler (1984) suggested two distinct patterns. In the eel, thrust is developed continuously along the body and generated by bending moment waves, which pass down the body from head to tail, with the wave on one side of the body lagging that on the other. In contrast, in the saithe, thrust is generated as discrete pulses at the tailblade, resulting from the generation of instantaneous maximum bending moments on alternate sides of the body. One consequence of the observed pattern in the saithe is that myotomal muscle towards the posterior (tail) lengthens when active and performs negative work for much of each tailbeat period. van Leeuwen *et al.* (1990), combining kinematics and electromyography of the slow muscle of carp with computer modelling of muscle function, came to a similar conclusion. Altringham *et al.* (1993) simulated *in vivo* activity patterns on isolated, superficial, fast myotomal muscle fibres from the saithe. Under conditions simulating steady swimming over a wide range of speeds, fibres at three locations along the body all performed positive work for much of each tailbeat cycle. However, as the wave progressed towards the tail, muscle fibres nearer the tail spent an increasing proportion of each tailbeat cycle performing negative work: at a tailbeat frequency of 12 Hz, net work near the tail was close to zero, since the initial negative work component was similar in magnitude to the positive work phase that followed. Similar studies by Rome *et al.* (1993) on scup, and Johnson *et al.* (1994) on largemouth bass, led to the conclusion that posterior muscles performed net positive work and that the models proposed for saithe and carp should be re-evaluated. It should be stressed that, in the analysis of van Leeuwen *et al.* (1990), whether or not net work was positive or negative depended upon which caudal position was studied: only those myotomes closest to the caudal fin performed net negative work. Furthermore, none of these studies addressed the problem of differences in body form and swimming mode. Since the body curvature wave (and hence muscle strain and

function) is determined by the interaction between the fish's body and the water, and the result of this interaction (swimming mode) is influenced by body form, it is important to try and view the whole picture.

We have taken published results and analysed a diverse data set, presenting it in a single format for comparison. The information needed for a complete analysis is not yet available, but sufficient is known to propose a model which shows how the existing observations fit into one complex pattern of variations and suggests avenues for future research.

Kinematics, electromyography and muscle function in seven species of fish

Fig. 1 summarises what is known or can be reasonably predicted about kinematics and muscle function from EMGs in seven species of fish. The lateral views of these fish are drawn to scale and provide an impression of the lateral surface interacting with the water during swimming. The dorsal and ventral fins of the trout, saithe and mackerel (and possibly carp and scup) would be held close to the body during steady swimming, and would not interact with the water. The wavelength present on the body during steady swimming at any time varies between $0.59L$ and $1.54L$ (where L is body length). The diagrams below the fish show the passage of the waves of curvature down the body in relation to muscle activity (myogram) during one tailbeat period T . The horizontal line at $T=0$ marks the start, and at $T=1$ the end, of one cycle. The horizontal axis represents the body length between head ($L=0$) and tail ($L=1$). The sets of diagonal lines in each diagram represent left-side muscle strain phases during the swimming cycle. The sequence of changes in muscle strain at each point on the left side of the body is followed in time, starting from mean length while lengthening ($0/360^\circ$) and passing through maximum (90°) and minimum (270°) strains before completing the tail beat. The diagonal nature of the lines shows the passage of the wave along the body.

In order to compare the published data, we have assumed that the wave of displacement of the body during steady-speed swimming travels at a constant speed. The detailed kinematic studies of saithe and mackerel, derived from sequences of whole-body outlines during steady swimming, have shown that the wave of body displacement travels at a constant speed (Videler and Hess, 1984, Fig. 4). The straight lines of body displacement in the eel are based on eight marked body points (Grillner and Kashin, 1976, Fig. 1). In carp, the body wave progresses steadily between positions three and eight but was slightly slower in the head (van Leeuwen *et al.* 1990, Fig. 4).

There is a progressive decrease in the number of waves on the fish bodies from left to right from 1.7 to 0.65 (wavelengths vary from $0.59L$ to $1.54L$), which is responsible for the clockwise rotation of the muscle strain lines. The heavy dashed line (90°) in each plot indicates muscle fibres reaching maximum length and the onset of shortening during the one completely depicted period T . Muscle is therefore lengthening in the blue zones and shortening in the yellow zones. The red

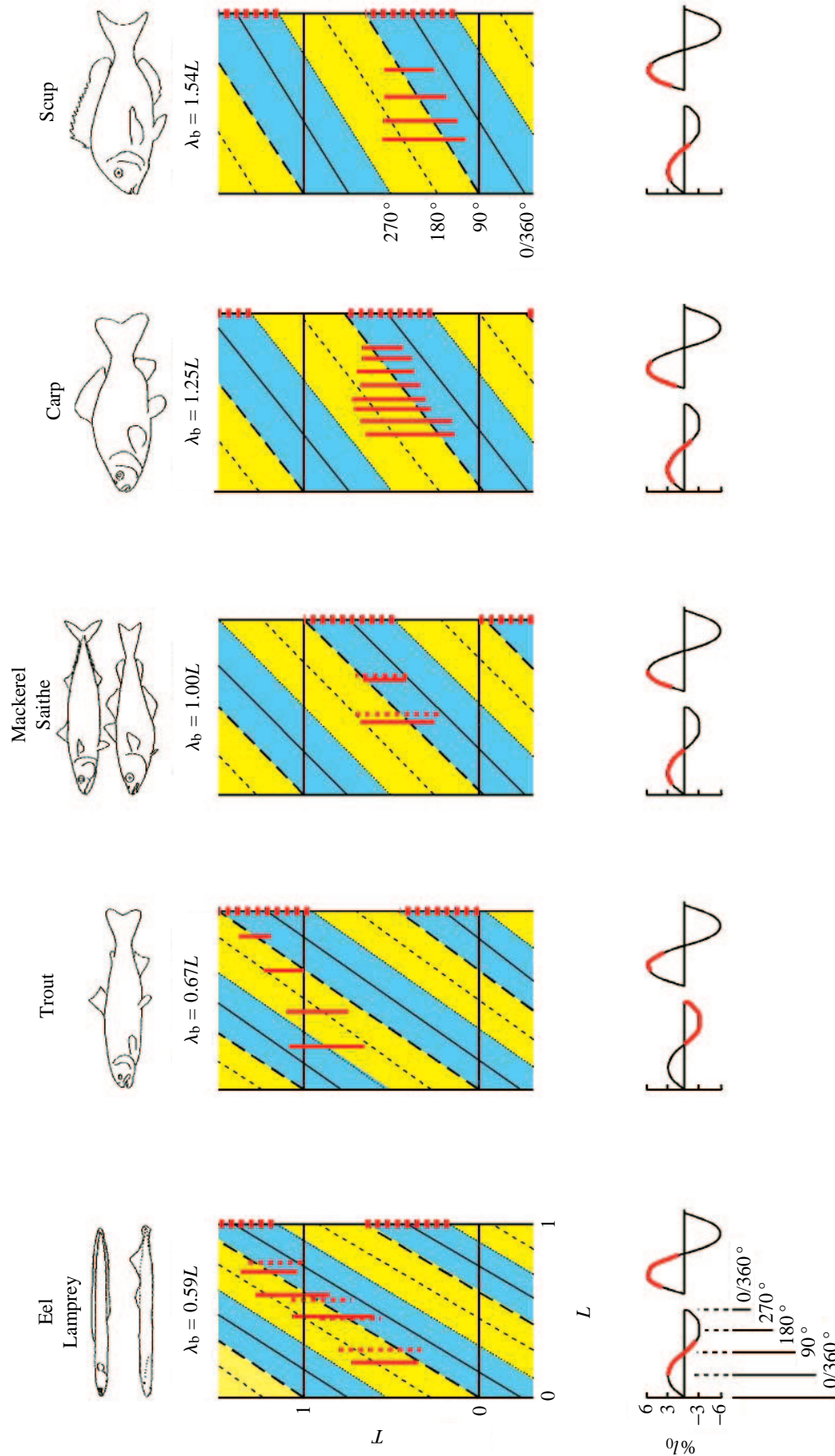


Fig. 1. Body forms of the seven species of fish studied are shown at the top. During steady swimming, the dorsal and ventral fins of the trout, saithe and mackerel are held close to the body. Beneath each body form sketch are diagrams representing the timing of the waves of curvature and electromyogram (EMG) duration during one tailbeat period T . The oblique lines in each diagram indicate the phases of the waves of curvature and the muscle fibre strain cycles. The phases are indicated on the left-hand side of the scup diagram and in the first strain cycle diagram, at the bottom left of the figure. The red vertical bars superimposed on the strain lines indicate the duration of EMGs at that position on the left-hand side of the body (EMGs of lamprey and saithe are dashed). Data are from superficial fast and slow

muscle fibres. The red dotted lines on the right-hand side of the diagrams indicate the duration of the tail beat from rightmost to leftmost. Further details are provided in the text: Wardle and Videler (1994) provide full details of how these diagrams were constructed. Below these diagrams are diagrams of muscle strain cycles of anterior and posterior muscle fibres, with EMG durations shown by the thicker red part of the line. Muscle strain and EMG patterns are derived from Grillner and Kashin (1976) (eel); Williams *et al.* (1989) (lamprey and trout); Hess and Videler (1984) and Wardle and Videler (1993) (mackerel and saithe); van Leeuwen *et al.* (1990) (carp); and Rome *et al.* (1993) (scup). λ_b , wavelength of body curvature, expressed in body lengths L ; $\%l_0$, percentage of mean fibre length.

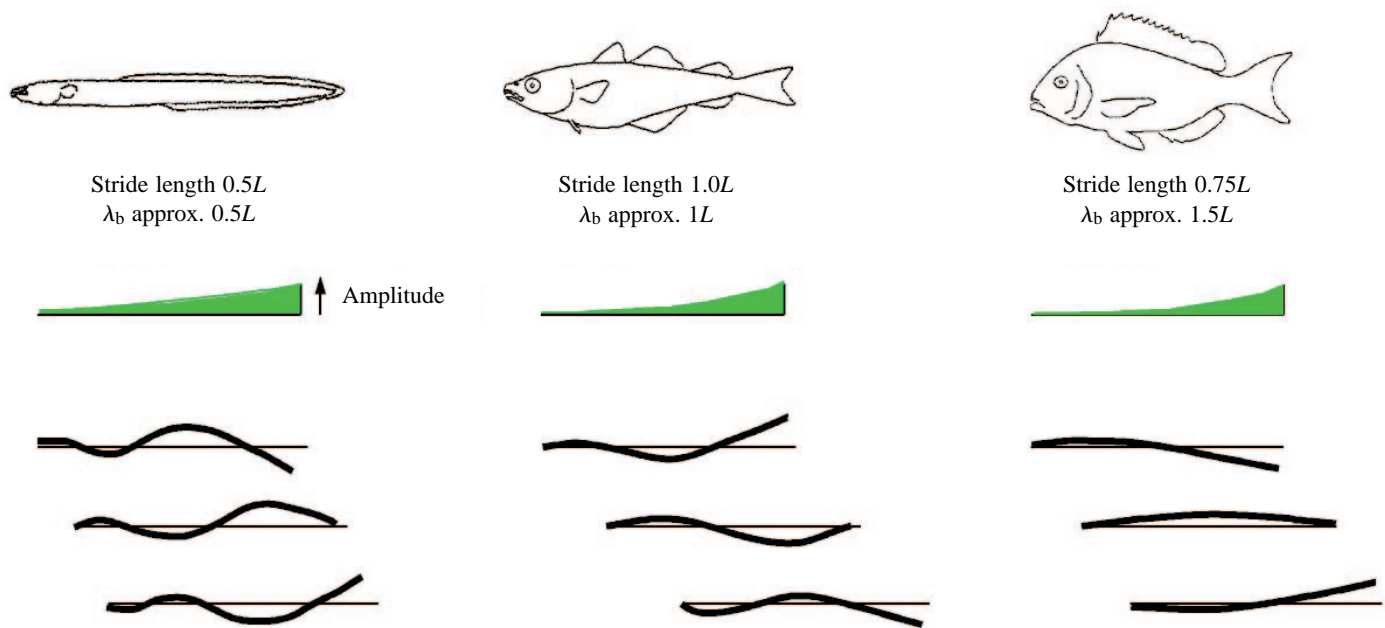


Fig. 2. Body kinematics and approximate stride length during steady swimming in eel, saithe and scup. λ_b , wavelength of body curvature, expressed in body lengths L . The maximum amplitude of the lateral excursions as a function of the position on the body from head (left) to tail (right) is indicated by the green areas. The lower three diagrams represent the forward displacement of the centre line of the body at three extreme positions during a tail beat from right (bottom) to left (top). The tail tip passes through the path of the swimming direction in the middle diagram for each species.

vertical bars superimposed on the strain lines indicate the duration of EMGs at that position on the left side of the body (EMGs of lamprey and saithe are dashed). Data are from superficial fast and slow muscle fibres. The tail tip cycle is indicated by the phase at the right-hand edge of each diagram. For example, where 90° strain meets the right-hand edge, the tail tip is fully left. The red vertical dotted lines at the right-hand edge of each diagram indicate the complete leftward sweep of the tail tip. Fish with tailblades produce peak power at the point where the diagonal $0/360^\circ$ phase lines (in the middle of the blue zones) meet the right-hand edge and the tip of the tail is crossing the fish's track, moving left.

In mackerel and saithe, the timing of the onset and end of the EMGs has been shown to be independent of swimming speed (Wardle and Videler, 1993). In other species, the number of sequences analysed was too limited to reveal the speed-dependence of EMG timing. Strain amplitude increases from front to back and is similar in all species studied: e.g. in the saithe it is $\pm 3\%$ mean fibre length (l_0) at $0.35L$ from the rostral tip, and $\pm 6\%l_0$ at $0.65L$ (Hess and Videler, 1984). Approximate strain amplitudes are given for the muscle fibres at the anterior- and posterior-most electrodes in each case (Fig. 1, lower diagrams). EMG duration is indicated by the red part of the cycles. Body kinematics are shown for eel, saithe and scup in Fig. 2. The maximum amplitudes of the lateral movements from head to tail are indicated by the green areas. The maximum amplitude increases linearly in the eel and as a power function in the scup. Saithe has a point on the body just behind the head where the maximum amplitude reaches a minimum, increasing rearwards from that point as a power

function. The lower diagrams schematically show three extreme positions of the centre line of the body for each species: tail tip extreme right, tail tip passing through the centre, and tail tip extreme left.

The amplitude of the lateral curvature determines the strain amplitude of the muscle fibres and influences absolute power output, but is not a factor in the following discussion.

The phase relationship between the EMG and the muscle strain cycle determines the pattern of force generation and work production by the muscle. The exact relationship between force generation and EMG activity is uncertain. Force generation will lag behind EMG activity by a period determined by the speed of contraction of the muscle. Time from stimulation to peak force ranges from 30 to 50 ms (Altringham *et al.* 1993; Davies and Johnston, 1993; Johnston *et al.* 1993; Johnson *et al.* 1994). Twitch contraction time of fibres from caudally placed myotomes is longer than from those more rostrally placed (Wardle *et al.* 1989; Altringham *et al.* 1993; Johnston *et al.* 1993; Rome *et al.* 1993). Thus, to a first approximation, force generation and EMG activity can be considered to be simultaneous when these short twitch contraction times are related to longer tailbeat periods. However, at high tailbeat frequencies, when muscles may be activated by only one to several action potentials in each cycle, force generation will lag behind EMG activity, and changes in contraction time along the body may become relevant. EMG activity between the 90° and 270° lines (the yellow zone in Fig. 1) indicates that the muscle is shortening during force generation, and thus is performing positive work. EMG activity between 270 and 360° (blue zone in Fig. 1) indicates that the

muscle is lengthening when active and thus is performing negative work, but will then perform positive work if force generation continues into the shortening phase. Since muscle relaxation will typically be about two times slower than activation (e.g. Altringham *et al.* 1993; Johnson *et al.* 1994), EMG activity that persists throughout shortening will lead to negative work being done when the muscle begins to lengthen.

Are there any features common to all species? With the exception of the trout, in all species, at all locations along the body, EMG activity begins before the 90° line, i.e. before the muscle begins to shorten, and ends long before shortening is over. This timing of EMG activity ensures that, in all these species, much of the force generation phase occurs when the muscle is shortening and thereby that the muscle performs positive work. Again, in all but the trout, the onset of EMG activity in the more anterior myotomes occurs just before the onset of shortening: in other respects, the pattern varies between species and each pattern needs to be considered separately.

In saithe and mackerel, rostral myotomes function as power generators, since muscle is active primarily during shortening. Progressing caudally, EMG activity occurs earlier, during the late phase of muscle lengthening and the early phase of shortening. Muscle nearer the tail therefore spends a greater part of the tailbeat cycle transmitting to the tailblade the power generated by more rostrally placed myotomes – extending active muscle is very stiff – before generating positive power as part of the wave of power positioning the tailblade during the later part of its sweep. Therefore, most of the body does not interact with the water, but passes power generated by the muscle down the length of the fish to produce thrust only at the tailblade. This model is consistent with widely accepted models of carangiform swimming (Lighthill, 1971). The tendons present in the caudal peduncle of tuna are more suitable than muscle for transmitting large forces at low energetic costs but have one important disadvantage. Tendon can only be used to transmit high forces and not for other purposes. Muscles in the caudal peduncle of typical fish are extremely versatile and greatly improve manoeuvring performance (Videler, 1975).

The eel and lamprey both lack tailblades and in both there is no significant change in EMG/strain phase shift along the body (Fig. 1). Work loop studies (e.g. Altringham and Johnston, 1990a,b) indicate that EMG activity late in extension and during shortening, as seen in these two species, will typically yield close to maximum positive power over a tailbeat cycle. As yet, empirical data are not available to confirm this hypothesis for these species. Power generated by the muscle will be passed directly to the water along most of the body length, with the aid of the erect dorsal and ventral fins (Fig. 1). These fish have more than one wave of curvature along their length (Fig. 2), and thus thrust is generated continuously by the undulating body from head to tail, in contrast to the pulsed pattern seen in fish with a caudal peduncle.

The carp (Fig. 1) appears to be similar to the mackerel and saithe: although it has only 0.80 waves on the body rather than

1.0, thrust is produced at the tailblade in two pulses, by the same mechanism used in mackerel and saithe (Hess and Videler, 1984). Muscle function in the carp was modelled (van Leeuwen *et al.* 1990), and not determined empirically, so there is still some uncertainty about just how muscle function changes along the body. In the scup (0.65 waves on the body), most of the power is generated by muscle in the caudal half of the body (Rome *et al.* 1993), but the overall pattern of muscle function is fundamentally similar to that of the saithe (Figs 1 and 3).

Instantaneous power curves and work loops

Instantaneous power curves for saithe are illustrated in Fig. 3B for muscle at three points along the body, over two tail beats. Strain and stimulation parameters simulated those *in vivo* during steady swimming (Altringham *et al.* 1993). Although no work loop data are available for mackerel, with a similar EMG timing during steady swimming to saithe (Fig. 1), we predict that they will exhibit a similar pattern of muscle function. Similarly, in Fig. 3C, instantaneous power curves have been calculated for muscle from three positions on the scup, from published force and length records (Rome *et al.* 1993), for comparison with the saithe. Fig. 3A shows preliminary data from trout slow muscle (L. Hammond, unpublished results). Stimulation parameters simulate EMG timings between those of the eel and saithe (see Concluding remarks). In all three species, power is generated as a caudally travelling wave. Muscle at all locations has both positive and negative work phases, with the relative magnitude of the negative work phase increasing towards the tail. Negative work production by the more caudal myotomes coincides with the power-generating phase of rostral myotomes and stiffens the muscle here to help transmit this power to the tail (Altringham *et al.* 1993). However, the more caudal myotomes of the scup spend less time transmitting, and more time generating, power than those in the saithe, although the pattern varies a little in saithe and probably in the other species too. The flattened body and the large dorsal and ventral fins of the scup distinguish it from the trout, saithe and mackerel, which all have rounded, streamlined body sections. The deep body and large fins of the scup may be important propulsive elements in addition to the caudal fin, in which case, although thrust is still generated as discrete pulses, these pulses may be lengthened to occupy a greater proportion of the tailbeat cycle. The number of waves on the body (and the number of vertebrae and myotomes) decreases in the order trout>saithe>scup, increasing the overlap of the power curves from Fig. 3A to Fig. 3C.

Concluding remarks

A trend that links body form and swimming mode to patterns of muscle function emerges from the analysis of these studies. Tail-less fish (eel and lamprey) with more than one wave of curvature on the body transmit power to the water along their whole length. EMG duration and the phase relationship

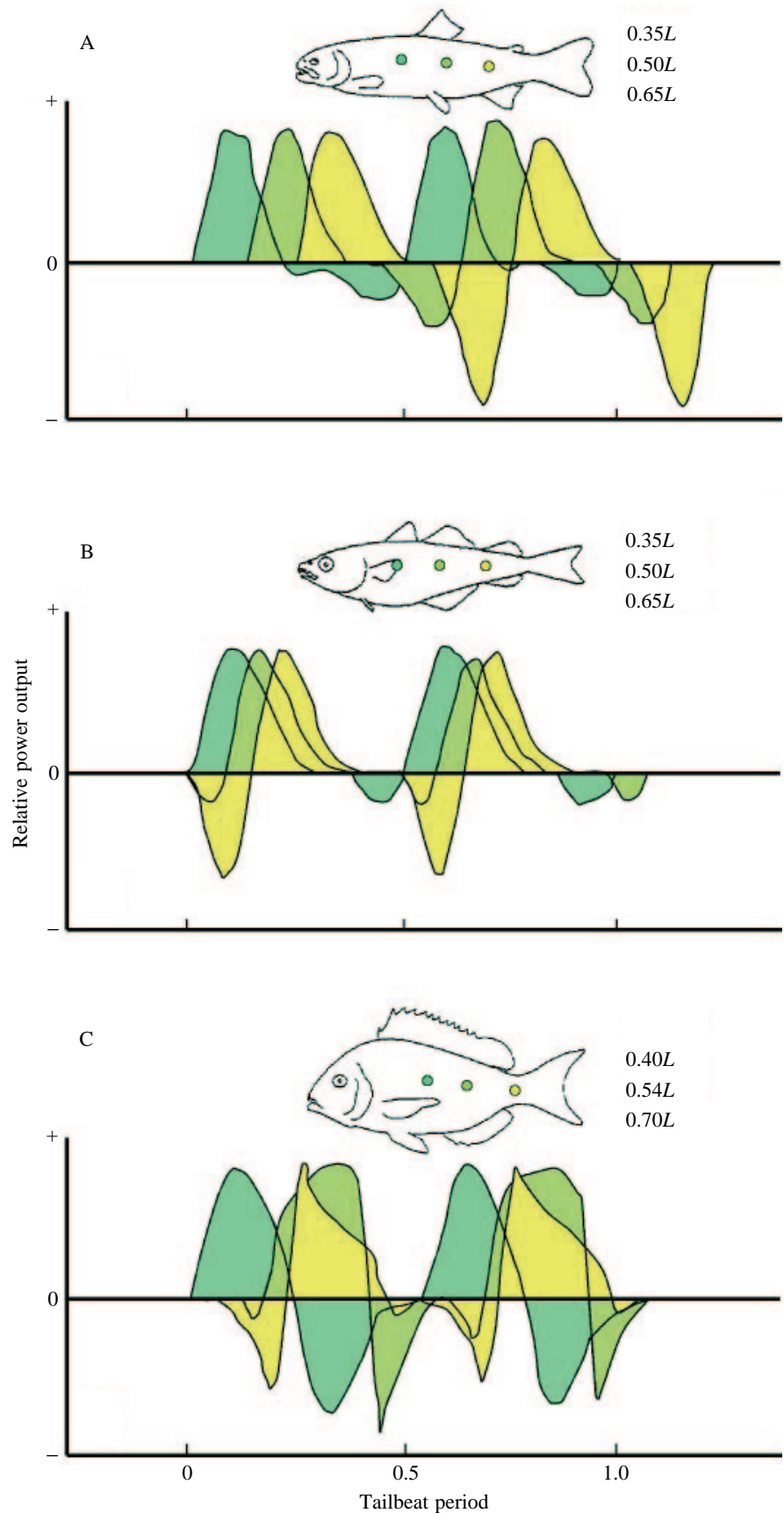


Fig. 3. Instantaneous power curves over two tail beats for the trout (A), saithe (B) and scup (C). Results are taken from muscle preparations from three locations on the body of each species, given as a proportion of body length L , from the rostral tip (e.g. $0.35L$). The figure illustrates the differences in time course of power output: no corrections have been made for variation in muscle preparation dimensions, and the magnitude of the power generated cannot therefore be compared: maximum values are scaled to the same height. Curves for trout were determined by L. Hammond (unpublished) results. Data for saithe are from Altringham *et al.* (1993) and Wardle and Videler (1993). Curves for scup were calculated from data published in Rome *et al.* (1993). The rapid transients in the $0.54L$ and $0.70L$ power curves for scup are due to the use of sawtooth rather than sinusoidal strain waveforms by Rome *et al.* (1993). Analysis of the strain waveforms published in Rome *et al.* (1993) and sonomicrometric measurement of muscle strain in saithe (L. Hammond, J. D. Altringham and C. S. Wardle, in preparation) suggest that the strain cycle is sinusoidal during steady swimming.

between the muscle strain cycle and EMG activity vary little along the length of the body. Fish swimming with a narrow, streamlined caudal peduncle and tailblade (saithe and mackerel) swim with one wave on the body, and thrust is generated mainly at the tail. There are marked changes in EMG duration and the EMG/strain phase relationship along the body. Caudal muscle not only generates positive work, it also helps to transmit power to the tailblade during the negative work phase. The scup perhaps illustrates the subtlety and complexity of fish swimming and the importance of all aspects of body form.

A number of uncertainties remain unresolved. All of the estimates of muscle strain used in this paper were inferred from changes in body curvature. The internal connections and myotomal overlap are 'designed' to allow some internal movement; indeed, Covell *et al.* (1990) have shown that in fast starts in trout local bending precedes local fast muscle shortening. Although such shifts are likely to be small or absent for superficial fibres during steady swimming, it is desirable that future studies measure muscle strain directly, using techniques such as sonomicrometry. Caution must also be exercised in making EMG recordings. Jayne and Lauder (1995) noted significant heterogeneity in EMG onset times with depth (at a particular location on the fish) due to the sequential activation of overlapping motomes.

Where the 0/360° phase line meets the right-hand margin of each diagram in Fig. 1, the tail tip is sweeping towards the left and is just crossing the centre line of the swimming track of the fish. Power output shows a peak at this same instant (Videler and Hess, 1984; Tang and Wardle, 1992), which in turn has been shown to coincide with a peak in work output from more rostral muscle and the coincident peak in force of more caudal muscle (Altringham *et al.* 1993). The same time was identified as a single instant of maximum bending moment all along the left side of the body (Videler and Hess, 1984). In the diagrams for carp and scup, which are admittedly based on minimal kinematic information, the tail tip is passing this point of maximum power output before the muscle on the left side has completed its active cycle, suggesting that the wavelength or the phase relationships may need further critical study. Can such fish, which put thrust pulses through the tailblade, have anything other than one complete wave of muscle strain cycle within the length of the body, and is this wave always identifiable in kinematic studies of stiff-bodied fish? In contrast, in the eel and lamprey, the maximum lateral body motion (0/360°, solid line, blue band, Fig. 1) follows the muscle activity of the zone just ahead in a regular pattern all the way to the tail tip, confirming the idea of continuous thrust output.

The phase relationship between force generation and the strain cycle is critical, but the appropriate mechanical studies have been carried out on few species for which we have EMG and muscle strain data. We know that contractile properties, such as contraction time, can change along the length of a fish (Altringham *et al.* 1993; Davies and Johnston, 1993; Johnston *et al.* 1993; Rome *et al.* 1993) and, if these changes are large, they will, at higher swimming speeds, interact with the EMG/strain relationship to determine how the muscle functions.

Surprisingly, there are few studies of trout swimming. From the published data, trout appear to be something of an anomaly. Although most of the thrust appears to be generated as a pulse at the tailblade, some proportion of it may be continuously passed to the water by the moving wave, because there is more than one wave on the body. Therefore, it is likely that trout have an EMG/strain pattern between that of eel and saithe, or perhaps more similar to that of saithe than to that of eel. However, EMG onset in trout is very much later in the tailbeat cycle than that of other species (Fig. 1). The EMGs in Fig. 1 would be compatible with results from other species, and fit the expected trend, only if they occurred more than 90° earlier in the tailbeat cycle. Work loops and instantaneous power curves generated by trout slow muscle fibres using the observed *in vivo* EMG/strain parameters yield patterns of power generation difficult to reconcile with any model: those using parameters mid-way between the patterns seen in eel/lamprey and saithe/mackerel (Fig. 3A) are very similar to those obtained from saithe (L. Hammond, unpublished results). The trout clearly requires further investigation.

This analysis is confined to steady swimming – fish swim in many different ways. Saithe could swim more like scup by erecting their dorsal and ventral fins, and trout could swim more like eels by using the same manoeuvre when changing speed or direction. Fish rarely swim steadily and on-line measurement of EMG activity and muscle strain (using sonomicrometry) shows that there are constant and dramatic changes in muscle function (L. Hammond, J. D. Altringham and C. S. Wardle, in preparation). It is important that future studies define swimming patterns exactly.

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